

SHIPWRECKS ON SANCTUARY SHORES:
DISTURBANCE AND RECOVERY ALONG A ROCKY
INTERTIDAL EXPOSURE GRADIENT

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Abstract

Recovery rates and processes were assessed along a rocky intertidal height gradient impacted by a shipwreck in Monterey Bay, California. This anthropogenic disturbance, fractured and scoured rock surfaces, was used to determine if recovery rates varied inversely with tidal height due to reduced abiotic stress from reduced exposure to air. Disturbed and control (undisturbed) plots were established in a mid/high intertidal red algal dominated by *Endocladia muricata* and *Mastocarpus papillatus*, mid intertidal mussel (*Mytilus californianus*), and low intertidal surfgrass (*Phyllospadix* spp.) assemblage. Percent cover of sessile organisms in 0.25 x 0.25-m plots in each of the assemblages was assessed between 1996-1998 and 2001-2002. Recovery rate was measured as the temporal change in the difference in similarity between disturbed and control plots. Ephemeral seaweeds initially colonized all disturbed plots, but were replaced by later successional species within 2-12 months. Contrary to expectation, recovery rate did not vary inversely with tidal height: it was greatest in the high intertidal red algal assemblage, followed by the surfgrass and *Mytilus* assemblages. The patterns of recovery suggest that assemblages characterized by a few dominant species that recruit rapidly and grow quickly (the red algal assemblage) will recover faster than those dominated by species with variable, episodic recruitment (mussel beds), or those that have limited success with sexual versus vegetative propagation (surfgrass). Life history features may be more important predictors of recovery than stress.

Introduction

Physical disturbance from natural and/or anthropogenic processes in the rocky intertidal zone is common. Natural disturbances include rock shear, sand scour, sediment burial, rolling boulders and wave action, while typical anthropogenic disturbances include shipwrecks, oil spills and trampling (Foster et al. 1988, Sousa 2001). The effects of disturbance, or “the damage, displacement, or mortality caused by physical agents or incidentally by biotic agents” (Sousa 2001), on the structure of marine communities are well documented (Dayton 1971, Lubchenco and Menge 1978, Foster et al. 1988, Sousa 1979, 1980, 2001), and research indicates disturbance is particularly important as it removes resident organisms, generating cleared space which can then be colonized by a variety of other organisms inhibited by residents prior to the disturbance. Disturbance effects and associated successional processes are difficult to predict because disturbances are, however, variable and the communities impacted are complex and dynamic (Sousa 2001).

Variation in the degree of disturbance including size, frequency, severity, and timing of disturbances can be largely responsible for differences in community response, including species composition (Sousa 2001). The few existing experimental studies of disturbance characteristics have focused on effects of size and intensity. Studies of disturbance size indicate increased grazer activity in small cleared areas and on the edges of large clearings reduced algal abundance during recovery (Paine and Levin 1981, Sousa 1984, Farrell 1989). Disturbance size can also affect recruitment and post settlement mortality (Dudgeon and Petraitis 2001), and recovery tends to be longer for large vs. small disturbances (Diether 1984). As disturbance intensity increases, damage increases, and recovery rates slow (Sousa 1980). DeVogelaere (1991) found that successional pathways were influenced by disturbance severity; early and mid successional species were abundant following severe disturbances (e.g. complete clearing), but disturbance resistant, late successional

species were more abundant after less severe disturbances (e.g. removal of upright parts of organisms). These and other variations in disturbance regimes can also affect species diversity (Sousa 1979, Keats et al. 1985), patch persistence (Paine 1979) and recruitment (Blanchette 1996).

Foster et al. (1988), Sousa (2001), and Foster et al. (2003) concluded that given the numerous biotic and abiotic processes, and their interactions, that affect marine communities it seems unlikely that generalized models based on these factors will be useful in predicting successional pathways at a particular site once a community is disturbed. Moreover, changes in processes other than those related to the removal of resident species (e.g. competition for space and other resources, grazing, and predation) can impact community recovery following disturbances. Season of disturbance is an important determinate of successional pathways (Foster et al. 2003), as well as the life histories of species involved (Sousa 1980). For example, algae and marine angiosperms often reproduce and recruit seasonally (Turner 1983a, 1983b, Sousa 1980); the timing of disturbance relative to reproduction could cause variable recovery. Foster et al. (2003) showed that *Endocladia muricata* recruitment and persistence in high intertidal zones dominated by the red algae *Endocladia muricata* and *Mastocarpus papillatus* at six sites along central California was greater in spring clearings, while *M. papillatus* recruitment and persistence was greater in fall clearings. Season of disturbance and differences in reproductive phenology of the two species were associated with these different patterns. The extent of propagation via vegetative vs. sexual reproduction also affects recovery rates (i.e. recovery may be delayed if colonization is solely dependent upon sexual reproduction; Sousa 1980, Dethier 1984, Turner 1985). The proximity and dispersal potential, as well as type of species surrounding a disturbed area may potentially influence rates and pathways of recovery (Kay and Keough 1981, Turner 1983a, Sousa 1984, Farrell 1989, Dudgeon and Petraitis 2001).

Tolerance of species to grazing and physical conditions may also alter successional trajectories (DeVogelaere 1991, Dudgeon and Petraitis 2001) and grazers have the ability to modify the series of species replacements (Foster 1992). Grazers that preferentially feed on early successional species can potentially accelerate recovery by reducing competitive exclusion of species, while grazers that consume later successional species may delay succession and allow ephemerals to persist (Farrell 1991, Sousa and Connell 1992). As discussed above, these effects will vary depending on grazer activity, and thus the size of the disturbed area and associated edge effects (Farrell 1989).

The importance of variable recruitment to community structure and succession has been reported for many invertebrates including mussels, barnacles, and sea urchins (see Foster et al. 1988 for review). Episodic recruitment of these and other invertebrates are likely to directly influence successional processes by pre-empting space that would otherwise be available for colonization. Recruitment pulses of herbivores, such as urchins, may influence successional patterns by altering algal abundance. Experimental removal of urchins results in the rapid re-colonization of macroalgae suggesting they can have large effects on algal colonization and abundance (Paine and Vadas 1969). These effects may be variable depending upon if grazers are specialists.

Recovery of intertidal assemblages following disturbances could also vary with tidal height. Few quantitative studies have examined this potential variation, but given that low intertidal habitats are less exposed to environmental stresses than those in the high intertidal it is reasonable to expect that recovery may be more rapid at lower tidal heights because of relatively reduced exposure to air. In contrast to this model Turner (1985) found that recovery rates for low intertidal surfgrass were slow because seedling survival was low and plants re-established solely by vegetative growth.

Additional studies of variation in recovery rates along an intertidal exposure gradient are necessary to determine the relative importance of life history features versus abiotic conditions on recovery.

Many studies have examined succession and recovery associated with natural disturbance (see Sousa 2001 and above), but similar studies of human induced disturbance in the rocky intertidal are less common (Foster and DeVogelaere 1993). Knowledge from such studies, merged with that of natural disturbances, is essential not only to better understand causes of community dynamics, but also to better manage areas where human impact is likely, and to evaluate the need for restoration if impacts occur. Our objectives were to assess natural recovery rates of rocky intertidal habitat disturbed by a shipwreck, determine how these rates varied over an intertidal exposure gradient, and consider how species' life histories may influence patterns of recovery.

Methods

In April 1996 the F/V *Trinity*, a 51' steel hull seiner, capsized and ran aground on a rocky shore near Pt. Piños, Monterey, CA (Fig. 1). The shipwreck and subsequent salvage (by rolling the vessel landward through the intertidal) resulted in 251 m² (measured area of disturbance) of physical damage, and 287 m² of chemical damage (measured area with spilled diesel fuel and engine oil) to the surrounding rocky intertidal habitat, along the complete intertidal gradient including low intertidal surfgrass, mid intertidal mussel, and mid/high intertidal red algal assemblages.

Permanent plots were established at the site in May 1996 to examine recovery in each of the above three assemblages. Five 0.25 x 0.25 m plots physically disturbed by the shipwreck (granite surfaces cleaved/scoured to expose 100% bare rock) were established in the surfgrass assemblage, 5 in the mussel assemblage and 3 in the red algal assemblage. All plots were located on flat, relatively horizontal surfaces to limit variability and standardize sampling. Each disturbed plot was paired

with the nearest undisturbed plot (control) at a similar tidal height and slope. Since these plots were also affected by fuel and oil, an additional set of control plots were randomly established outside of the wreck site but in the same assemblages to control for the effects of possible chemical disturbance. Initial sampling of control plots outside the wreck site revealed no significant differences between them and the controls within the wreck site. Sampling of these plots was terminated after 2-24 months and the data are not reported here. Thus, the control plots within the wreck site functioned as the predisturbance condition and were compared to disturbed plots to assess recovery.

Percent cover of macroalgae and sessile invertebrates was determined in May and August 1996 and then at 6-month intervals between May 1996-December 1998 and May 2001-May 2002 using a point quadrat frame modeled after Foster et al. (1991). A metal rod was lowered through 30 random holes in a 0.25 x 0.25 cm clear plastic plate raised and centered above the sampling area and all sessile organisms contacted at each point were recorded. When algae were layered beneath a point, successive layers were recorded by moving upper layers aside. Multiple contacts of the same species were not recorded. When layering occurred total percent cover exceeded 100%. All algae were identified to the lowest possible taxon using *Marine Algae of California* (Abbott and Hollenberg 1976).

Analyses

Recovery of damaged assemblages was assessed using the Bray-Curtis Percent Similarity Index (Bray and Curtis 1957). Percent similarities between plots were compared instead of species percent cover because percent similarity enables a comparison of one plot to another with a single value based on all species and thus estimates “assemblage recovery.” To calculate the similarity of disturbed to control plots within an assemblage, the percent similarity of each damaged plot was

compared to each control plot (n=25 comparisons for *Mytilus* and surfgrass assemblages, n=9 for the red algal assemblage). ANOSIM (Clarke and Warwick 1994) was then used to assess recovery of each of the assemblages.

Regression analyses were used to determine if recovery rates varied among assemblages. The average percent similarity of disturbed plots relative to control plots was regressed against time for each of the assemblages, and differences in recovery determined from differences in slopes. The last data included in the analyses were those from the first sampling date in which no significant differences were detected between percent similarities of disturbed and control plots within an assemblage.

Results

Patterns of succession were similar in disturbed plots regardless of tidal height. Ephemeral algae including diatoms (mixture of *Berkeleya* sp., *Beelerochea* sp., and *Licmorpha* sp.) *Petalonia fascia*, *Porphyra perforata*, *Ulva* spp. (including former *Enteromorpha* sp.), *Urospora pencilliformis*, *Ulothrix pseudoflacca*, and *Chaetomorpha californica* colonized disturbed plots within two months in the *Mytilus californianus* (hereafter *Mytilus*) and surfgrass (*Phyllospadix* spp.; here after *Phyllospadix*) assemblages (Figs. 2B & 4B), while there was a four-month lag in their colonization of the mid/high red algal assemblage (Fig. 6B), during which time the plots remained 100% bare rock. Some of these ephemerals persisted for up to one year in the mid/high intertidal red algal (Fig. 6B) and *Mytilus* assemblages (Fig. 2B), while most were gone by December 1996 in the surfgrass assemblage (Fig. 4B). Ephemeral algae were also present in control plots in red algal, surfgrass, and *Mytilus* assemblages during the study, but they occurred episodically and their abundance was typically much lower than in the disturbed plots (Figs. 2A, 3A & 7A).

Later successional, perennial species began to re-colonize disturbed plots in all assemblages within a year of the initial disturbance. Species including *Endocladia muricata*, *Mastocarpus papillatus*, *Mazzaella flaccida*, and geniculate and non-geniculate corallines, which were abundant in red algal assemblage control plots (Fig. 6A), tended re-colonize disturbed plots most rapidly (Figs. 6B & 7B). *Phyllospadix* re-colonization within the surfgrass assemblage came entirely from new recruits, not vegetatively via rhizometous extensions, and took at least two years to occur (Fig. 4A) and its percent cover was still much lower in the disturbed plots than in controls at the end of the study (Fig. 4B). Red algae including geniculate corallines, *Cryptopleura* sp. and *Mazzaella splendens* became abundant prior to re-colonization of surfgrass, and remained so at the last sampling (Figs. 4B & 5B). Within the *Mytilus* assemblage *Mazzaella flaccida*, “*Petrocelis*,” and other red algal crusts, which occurred commonly as epiphytes on mussels in the control plots (Fig. 3A), were abundant attached to rock in the disturbed plots (Fig. 3B).

Sessile animals were also slow to re-colonize in all three assemblages. Within the red algal assemblage *Anthopleura elegantissima* colonized within one year (Fig. 7B), but was always less abundant than in control plots (Fig. 6A). *Mytilus* were first sampled in disturbed plots in December 1997, but accounted for less than 35% cover in May 2002, six years after the disturbance (Fig. 2B). *Balanus glandula* did colonize disturbed plots slightly faster than *Mytilus*, and its abundances were similar to those in controls within one year (Fig. 3A & 3B). Tunicates did not colonize the surfgrass assemblage until 5 years after the disturbance, and it took nearly two years for the tubeworm *Phragmatopoma californica* to colonize (Fig. 5B). These organisms were present in relatively high abundance in the surfgrass assemblage controls throughout the study (Fig. 4A).

Recovery of the low intertidal surfgrass, mid intertidal *Mytilus*, and mid/high intertidal red algal assemblages following the initial disturbance was variable. In general, recovery across all

three tidal heights was slow, with most disturbed plots taking greater than five years to recover. The red algal assemblage characterized by *M. papillatus*, its' diploid phase "Petrocelis," and *E. muricata* was considered recovered by December 1998, as no significant differences were detected between control and disturbed plots (ANOSIM, $r=0.37$, $p=0.10$) and plot similarity increased until sampling ended in May 2002 (ANOSIM, $r=0.04$, $p=0.40$). Although control and cleared plots within the red algal assemblages were similar, the abundance of "Petrocelis," *Mazzaella flaccida*, and *Anthopleura elegantissima* was always lower in disturbed plots (Fig. 7B) than in controls (Figs. 6A).

The surfgrass and *Mytilus* assemblages did not fully recover, although the similarity of individual disturbed to control plots occasionally fell within the range of percent similarities among control plots (Surfgrass: 1 in 5 plots during December '97, May '01, Dec'01; *Mytilus*: 1 in 5 plots during May '97, May '01, December '01, May '02). There were significant differences between the control and disturbed plots in the surfgrass (ANOSIM, $r=0.67$, $p=0.01$) and *Mytilus* assemblage (ANOSIM, $r=0.81$, $p=0.02$) at the end of the study in May 2002. Lack of recovery was primarily due to the limited re-colonization of dominant species in each assemblage. *Phyllospadix* and tunicates in disturbed plots never reached abundances found in control plots in surfgrass assemblage (Figs. 4A, 4B & 5B). Similarly, *Mytilus* cover was ~50% greater in control versus disturbed plots within the *Mytilus* assemblage, and disturbed plots still had an average of ~50% cover of bare space in May 2002, six years after the disturbance (Figs 2A & 2B).

Although the red algal assemblage was the only assemblage to recover, the *Mytilus* and surfgrass assemblages approached recovery at varying rates. Contrary to prediction, recovery rate did not vary inversely with tidal height. The red algal assemblage at the highest tidal level approached recovery most rapidly, followed by the surfgrass assemblage at the lowest tidal level. The *Mytilus* assemblage within the mid intertidal zone approached recovery the slowest (Fig. 8).

Discussion

Successional pathways were similar in all three assemblages with ephemeral algae persisting for a few months to a year, later successional algal species re-colonizing next, followed by sessile invertebrates (and *Phyllospadix* in the surfgrass assemblage). Similarity in the sequence of species replacements in each of these assemblages indicated successional stages during recovery were similar despite differences in species composition of controls and tidal height. Persistence of each successional stage was, however, variable. Particularly notable was the more rapid transition from ephemeral species to later successional species (*Egregia menziesii* and *Corallina* spp.) within the surfgrass assemblage. The rapid re-colonization of these two species is most likely related to their ability to colonize disturbed habitats, particularly those with reduced exposure to air at the lower tidal height.

The recovery of the red algal assemblage was related to the rapid re-colonization of dominant species within the assemblage. *Endocladia muricata*, *M. papillatus*, and “*Petrocelis*” crusts consistently dominated control plots in the red algal assemblage. *Mazzaella flaccida*, *Mazzaella affinis* and *Anthopleura elegantissima* were also present in variable, but relatively high abundance in control plots throughout the study. Of these six species, all but “*Petrocelis*” crusts and *M. affinis* re-colonized disturbed plots within a year. Life history traits including longevity (>80yrs old) slow growth and low recruitment (Paine et al. 1979) of “*Petrocelis*” may make this algal phase particularly slow to recover from disturbances. Despite the slow return of some species, *E. muricata* and *M. papillatus* were as abundant in disturbed plots as they were in controls in less than five years.

The relatively rapid recovery of the red algal assemblage has been reported at other disturbed sites along the California coast. Foster et al. (2003) examined recovery of *Endocladia* assemblages

at 6 sites along the California coast and found that most recovered within 6 years. Successional patterns at these sites were variable, but similar to those at our site: ephemerals, when present, were replaced by dominant perennials (*M. papillatus* and *E. muricata*) within a year.

Although the surfgrass assemblage did not fully recover six years after the disturbance the disturbed plots did converge on the control plots. Control plots were typically characterized by greater than 80% cover of *Phyllospadix* with a fairly stable understory of tunicates and *Phragmatopoma californica* (Figure 2A). Disturbed plots never developed greater than ~30% cover of *Phyllospadix* (Fig. 4B) and while *P. californica* cover did become similar to controls by the end of the study, tunicates were considerably less abundant than in controls (Figs. 4A & 5B). Increases in similarity between the control and disturbed plots was due these increases in surfgrass and invertebrates as well as increases in foliose red algae (i.e. *Mazzaella splendens*, *Cryptopleura* sp., *Prionitis* sp., and *Callophyllis* sp.) and geniculate corallines (*Calliarthron cheilosporioides*, *Bossiella plumosa* and *Corallina* spp.), in both plot types. Of these algae geniculate corallines, *Cryptopleura* sp. and *M. splendens* were more abundant in disturbed plots, while *Prionitis* sp. was a more common (as an under-story alga) in control plots.

It is likely that disturbed plots in the surfgrass assemblage were still in a mid successional stage, where competition among foliose red algae and geniculate corallines may have delayed recovery. These algae likely excluded the surfgrass by occupying space and preventing vegetative propagation from outside of the disturbed area. While these species occurred within the control plots they were not nearly as abundant as *Phyllospadix* and sessile invertebrates. Turner (1983a) also found that foliose algae (*Cryptosiphonia woodii* and *Rhodomela larix*) dominated disturbed surfgrass habitats in mid successional phases. These and other red algal species persisted for more than 3 years and delayed *Phyllospadix scouleri* re-colonization. Similarly, *Phyllospadix* remained

relatively rare through most of our study, and did not re-colonize until three to five years after the disturbance.

The delay in surfgrass re-colonization was expected given the size, and nature of the disturbance, and biology of surfgrass. Because the disturbance caused considerable rock fracture in this assemblage the disturbed habitat was isolated such that all re-colonization of surfgrass had to be from seeds, not vegetative growth. Numerous studies (Turner 1983b, Turner 1985, Turner and Lucas 1985) suggest that colonization of *Phyllospadix* spp. can be slow, especially when vegetative propagation is not possible, because of high seed and seedling mortality (Turner 1983a, Holbrook et al. 2000). Seeds are particularly vulnerable to crab and fish predation (Williams 1995, Holbrook et al. 2000). Seed germination and seedling establishment are also substrate specific requiring branched algae for attachment (Turner 1983b, Turner and Lucas 1985, Blanchette et al. 1999). Crabs (*Pachygrapsus crassipes* and *Pugettia* sp.) were present throughout the surfgrass zone during our study (although seed predation was not directly observed). Seed production and seedling mortality could have contributed to the slow recruitment of *Phyllospadix* and reduced recovery within this assemblage at Pt. Piños.

Reduced recovery within the surfgrass assemblage was also influenced by the slow return of colonial tunicates. These organisms were common as understory in control plots. They re-colonized only from new recruitment, not lateral propagation from fission of nearby adults. Life history studies of colonial ascidians suggest that these organisms reproduce readily by fission, but also reproduce sexually (Millar 1971, Durante and Sebens 1994). Thus, assuming local abundance is correlated with larval production, larval supply likely did not contribute to the reduced recruitment in disturbed plots except on a seasonal basis. Colonial ascidians have limited dispersal potential given their short larval duration (settlement within a few minutes to hours; Olson 1985, Jackson

1986), but disturbed plots were only 1-10m away from very large, undisturbed control areas so it seems unlikely that larvae did not reach disturbed plots. Reduced and slow recruitment of tunicates may be due to substrate specific recruitment (they do not recruit favorably to bare, horizontal surfaces; Gotelli 1987) or perhaps the abundant foliose algae in the disturbed plots made settlement and/or attachment difficult. Although we can only speculate on reasons for the delayed colonization of tunicates, results from our study clearly suggest that re-colonization and dominance of colonial ascidians within the *Phyllospadix* understory can be slow (3-6 years) when dependent solely on new recruitment.

The *Mytilus* assemblage never recovered, and approached recovery at the slowest rate. Slow recovery was probably because the assemblage was dominated by a single animal, *Mytilus californianus*, with variable recruitment. *Mytilus* were the primary space holders in the control plots, with most algae and associated barnacles occurring as epibionts. Following the disturbance *Mytilus* did not re-colonize immediately and after six years there was ~50% greater percent cover in control relative to disturbed plots. Bare space still dominated in disturbed plots (~50% cover in May 2002) and qualitative observations suggest grazers displaced most algal species that initially colonized.

The relatively low recovery of mussels was probably related to larval supply and post settlement mortality. Invertebrates are known to have variable larval supply, which can result in recruitment pulses. Additionally, these early life stages are vulnerable and can be advected away from suitable habitat, consumed by other organisms, or die if subjected to abiotic stress (Underwood and Keough 2001). These factors may explain why most *Mytilus* that colonized disturbed plots were not new recruits, but older individuals that spread in from adjacent, undamaged areas. When juveniles (presumably from larval recruitment) occurred in disturbed plots they were primarily in cracks or other protected areas. These observations suggest that despite the close proximity of adult

Mytilus, their larvae seldom settled and matured to adult size in disturbed plots. This could be due to episodic release and/or recruitment of larvae but if that were true, one would expect at least one recruitment pulse within the six-year study. Since this never occurred it is likely that any settled larvae died or were removed by filter feeders or predators. Either of these is possible given the observed patterns of recruitment from creeping mussels as well as those that recruited in cracks. Both patterns suggest reduced predation or stress from harsh environmental conditions by settling in the more heterogeneous habitat or under the shade of adult mussels.

The ability to recover, as well as the recovery rates themselves, in the red algal, surfgrass, and *Mytilus* assemblage was associated with the demographic features of the species that comprised each of the assemblages and the interactions among species, not the exposure gradient along which they were located. If reduced exposure and benign environmental conditions associated with the low intertidal zone were the most important factors influencing recovery, the low intertidal surfgrass assemblage should have recovered most rapidly, followed by the *Mytilus* assemblage, with the mid/high intertidal red algal assemblage recovering most slowly. Because recovery rates were actually fastest in the mid/high intertidal red algal assemblage, followed by the low intertidal surfgrass assemblage, and slowest in the mid intertidal *Mytilus* assemblage it is unlikely that recovery rates were driven by tidal exposure.

Many models have been proposed to explain successional processes in the intertidal. Facilitation and inhibition models proposed by Connell and Slater (1977) were not broadly applicable across the high, mid, and low intertidal habitats in this study. The surfgrass assemblage was the only assemblage in our study where inhibition (i.e. surfgrass excluded by dominant foliose algae) or facilitation (i.e. certain algal species resulted in favorable recruitment of surfgrass) may have been important in succession.

Perhaps all that can be predicted are relative rates of recovery for a particular assemblage given the types of organisms present. For example, assemblages with only a few dominant species, which recruit regularly and grow rapidly, are likely to recover most rapidly because of reduced interspecific competition, an ample supply of fertile individuals and reduced variation simply because fewer species are involved. Those assemblages that are characterized primarily by one habitat forming species (i.e. surfgrass) and a suite of understory organisms are likely to approach recovery at a slightly slower rate because of the potential for long-lived understory algae to delay succession in hospitable environments. Delayed recovery can also occur if sexual reproduction or larval/spore survival of dominant species is reduced. The more organisms (and the more variability in their recruitment success) that characterize an assemblage, the longer it will take for that assemblage to recover. Finally, when disturbed habitats are dominated by a single species that is characterized by variable recruitment (i.e. *Mytilus*) and high post settlement mortality, recovery will generally be slow as organisms creep back into disturbed habitats. During this time apparent alternate stable states may develop and persist, but if the habitat is not hospitable for other organisms it is likely that bare space will persist for some time.

Traditional models were not useful tools for predicting successional pathways. Communities are influenced by a variety of complex interactions among species, habitats and environmental factors. Our data indicate life history attributes must be incorporated into models of succession if such models are to make accurate predictions about natural communities. Ultimately this study suggests recovery from large disturbances can be slow, driven by the species' life histories that characterized each of the assemblages. Our results do not support the general model that recovery varies inversely with tidal height and exposure.

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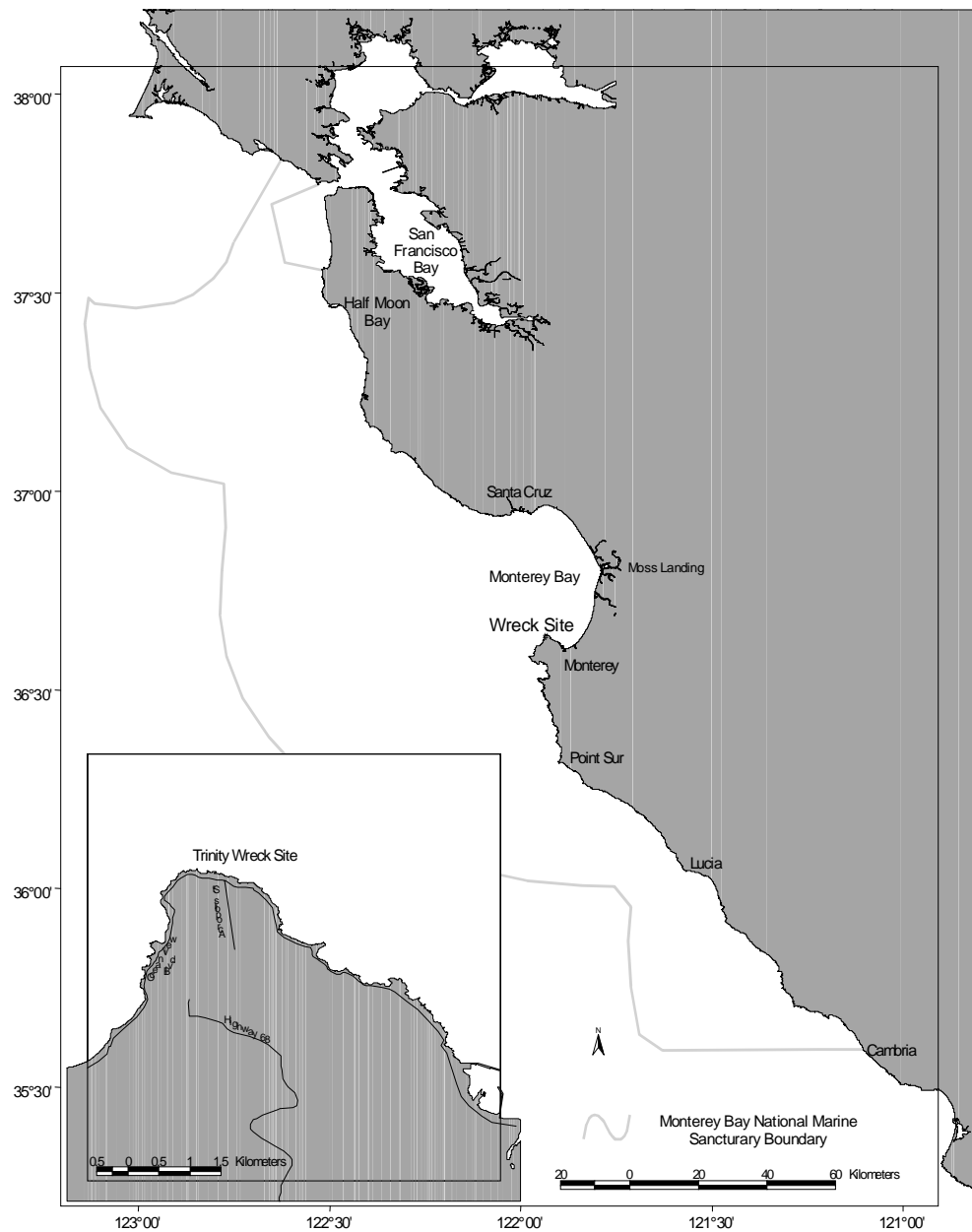


Figure 1. Wreck site, near the southern entrance to Monterey Bay, California.

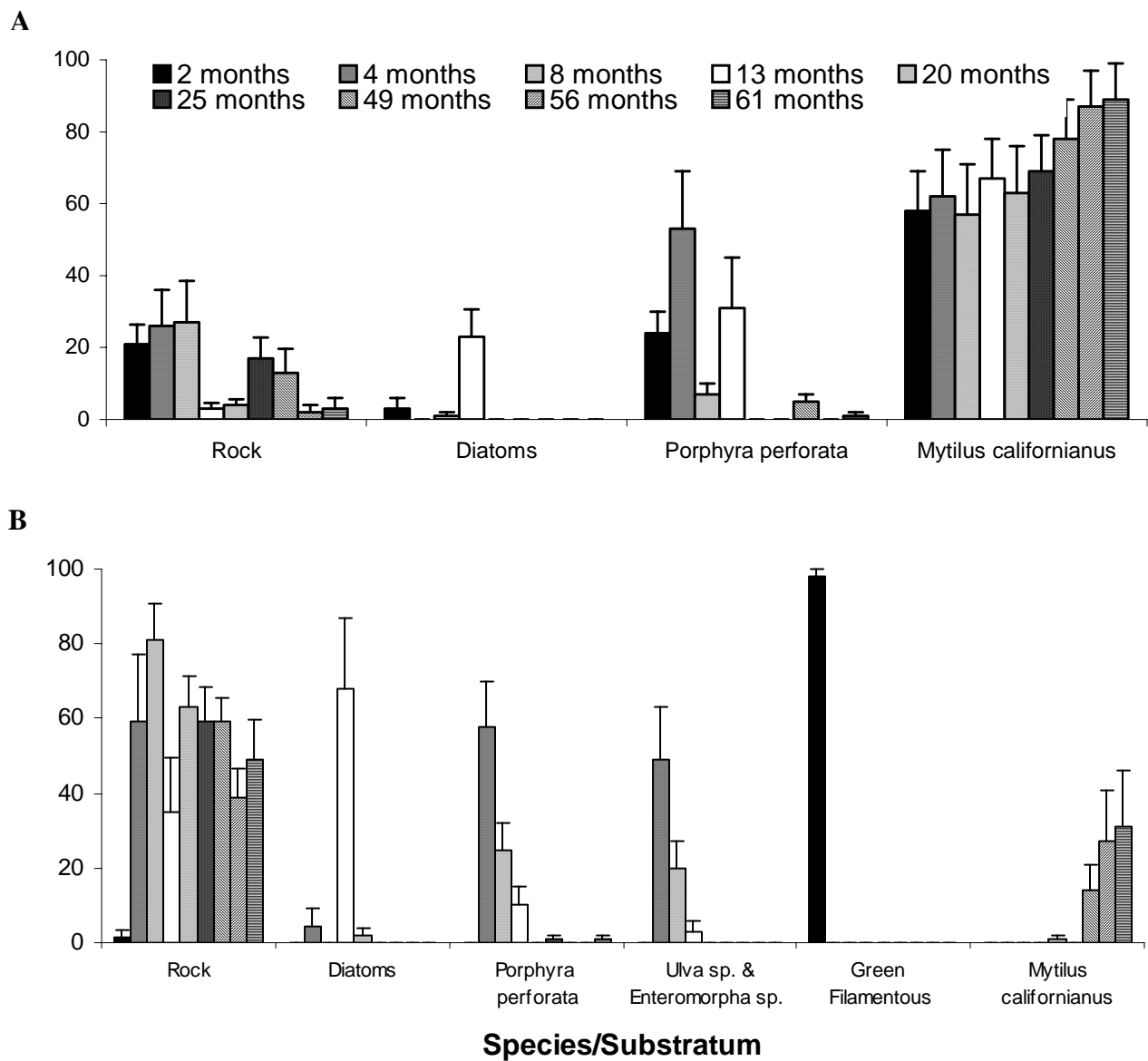


Figure 2. Percent cover (mean + SE) of species with cover's >20% in control (A) and disturbed (B) plots within the *Mytilus* assemblage between April 1996-May 1998 and May 2001-May 2002.

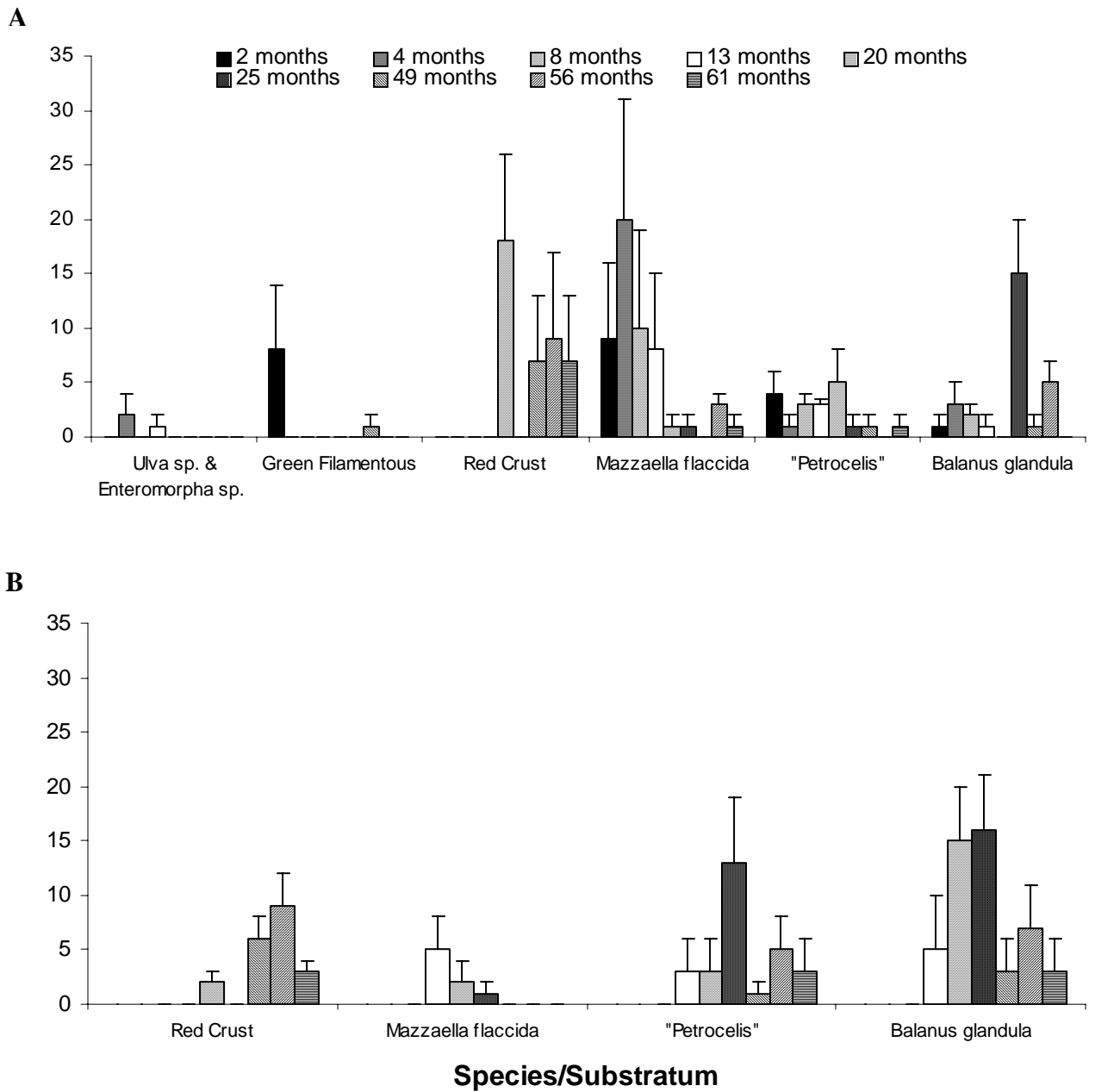


Figure 3. Percent cover (mean + SE) of species with cover's <20% in control (A) and disturbed (B) plots within the *Mytilus* assemblage between April 1996-May 1998 and May 2001-May 2002.

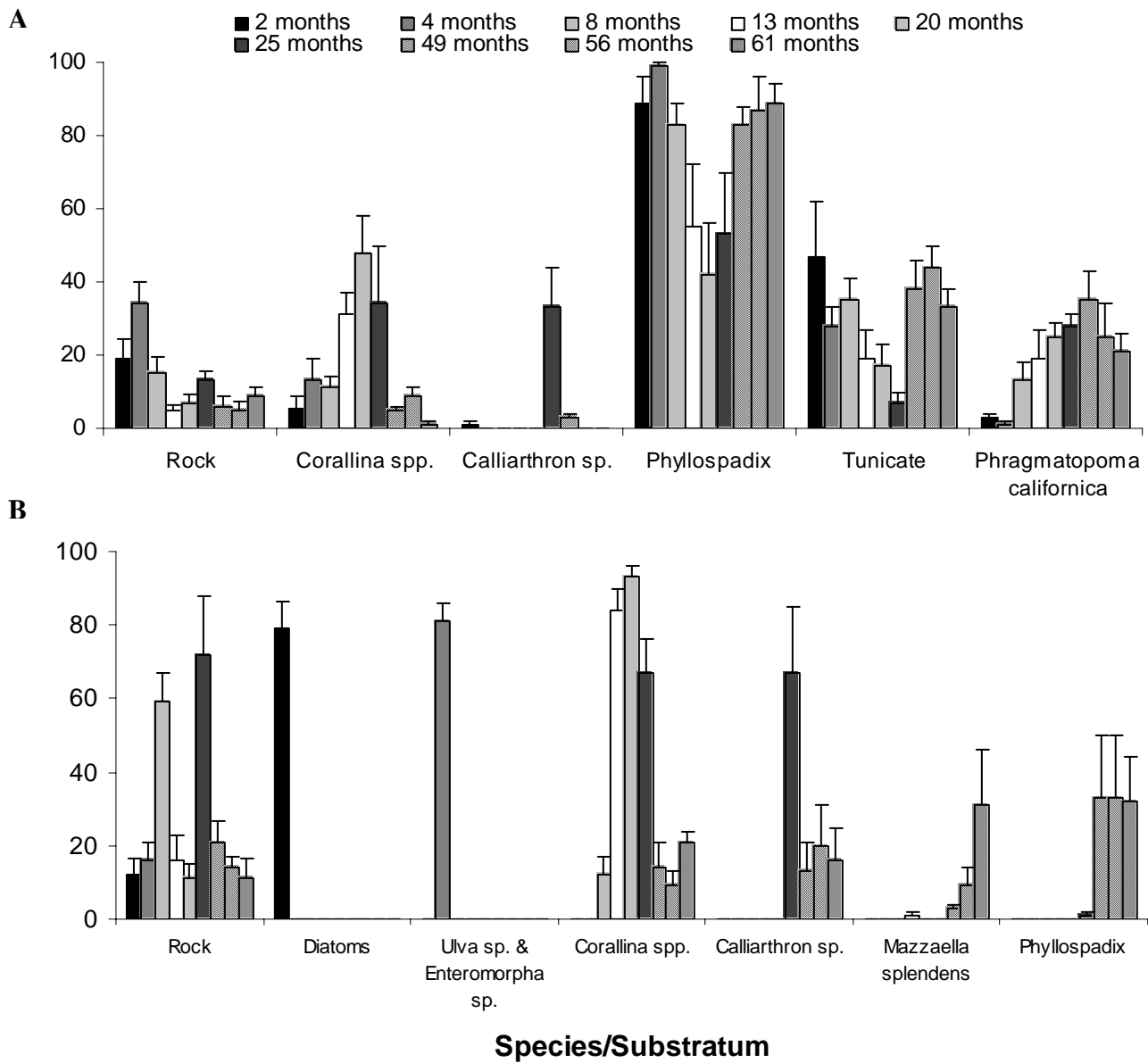
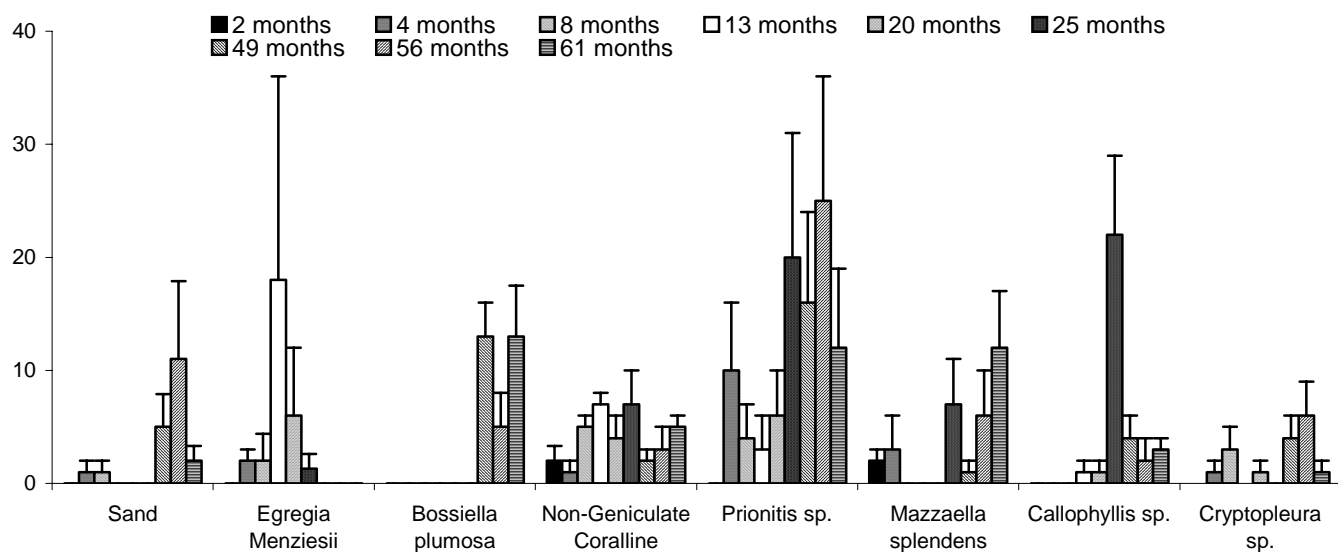


Figure 4. Percent cover (mean + SE) of species with cover's >30% in control (A) and disturbed (B) plots within the surfgrass assemblage between April 1996-May 1998 and May 2001-May 2002.

A



B

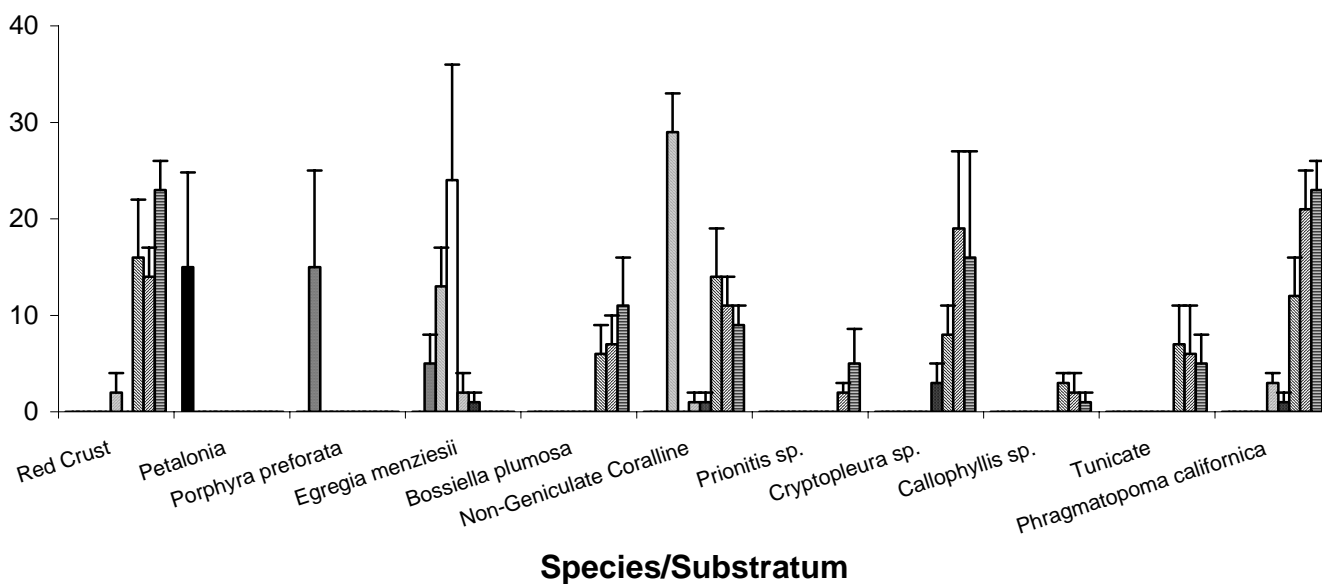


Figure 5. Percent cover (mean + SE) of species with cover's <30% in control (A) and disturbed (B) plots within the surfgrass assemblage between April 1996-May 1998 and May 2001-May 2002.

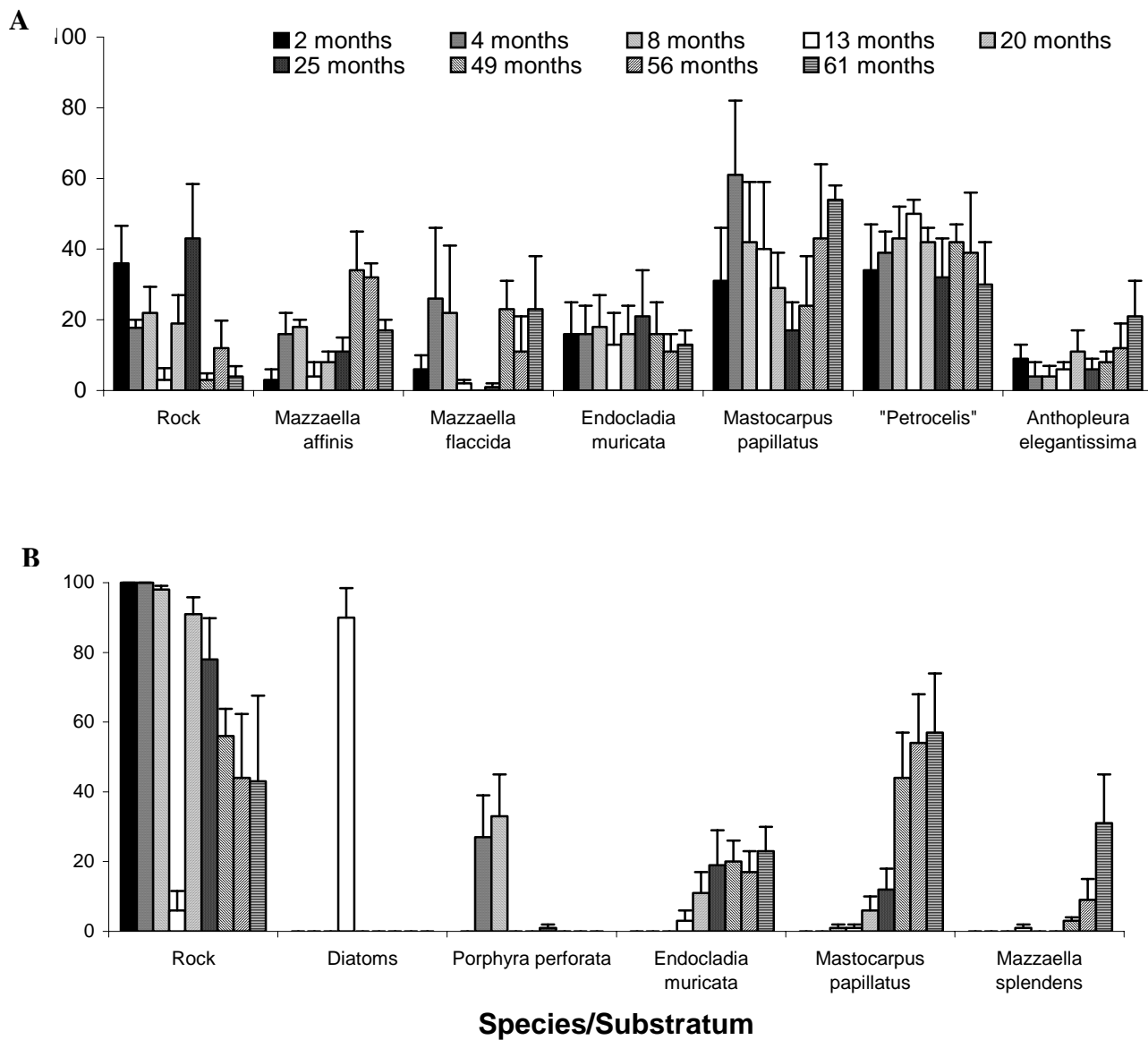


Figure 6. Percent cover (mean + SE) of species with cover's >20% in control (A) and disturbed (B) plots within the red algal assemblage between April 1996-May 1998 and May 2001-May 2002.

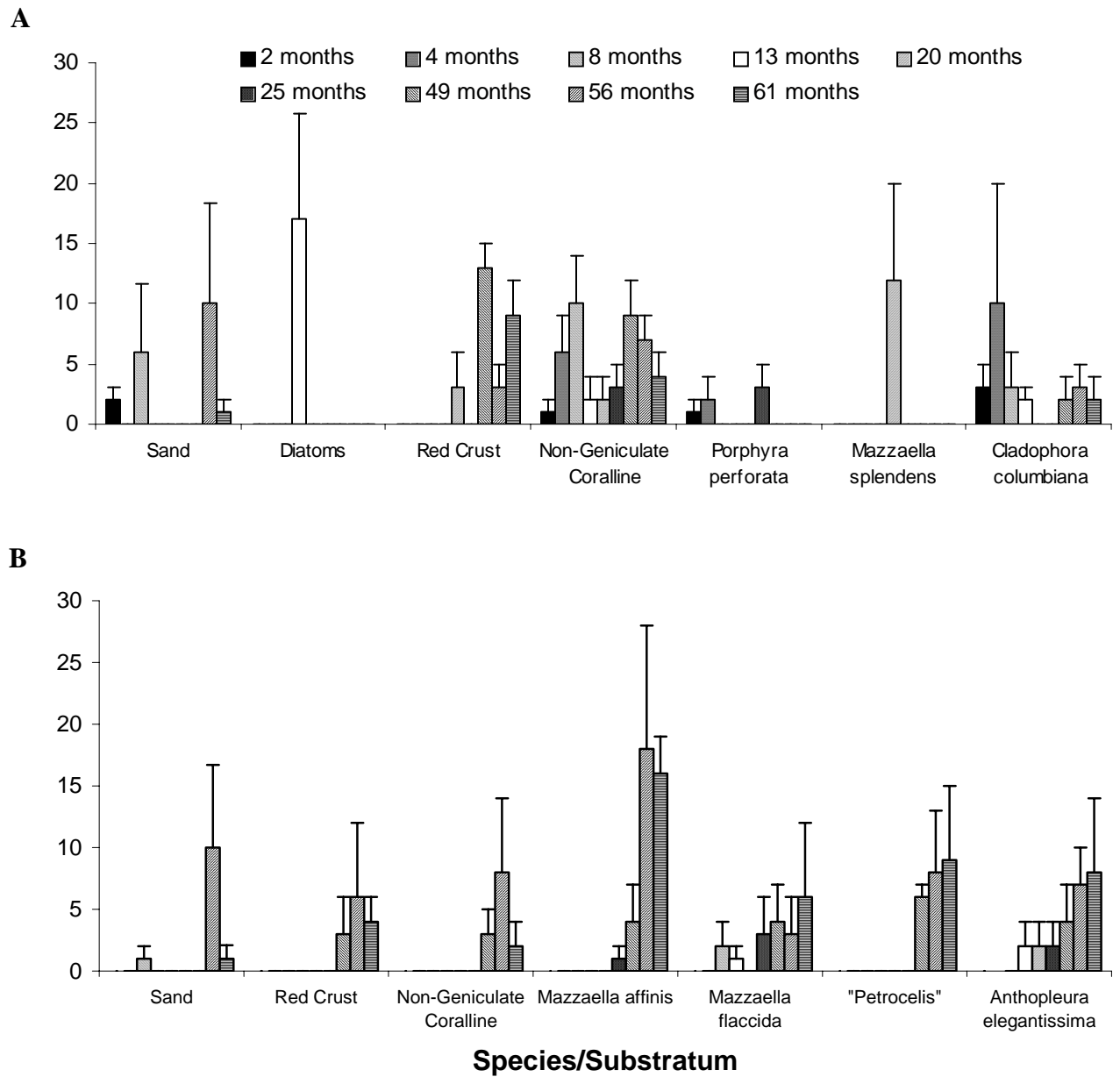


Figure 7. Percent cover (mean + SE) of species with cover's <20% in control (A) and disturbed (B) plots within the red algal assemblage between April 1996-May 1998 and May 2001-May 2002.

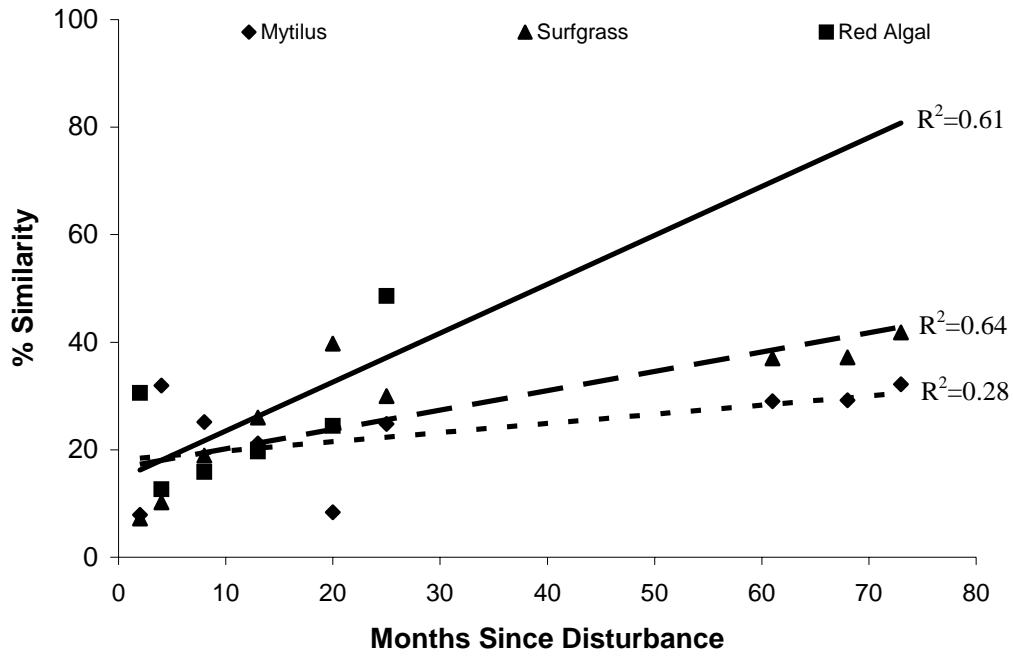


Figure 8. Mean percent similarity of disturbed to control plots within the *Mytilus*, red algal, and surfgrass assemblages since the disturbance. Slope of each line represents the relative recovery of each assemblage.

Appendix-

Management Considerations

Data Management

More careful collection and maintenance of data sets are required. If there is the potential for long-term monitoring, it is in the best interest of the project for the Monterey Bay National Marine Sanctuary (MBNMS) to receive copies (hard and disk files) of the report, data, and analyses for future reference. This is particularly true if the MBNMS employs an independent party (i.e. someone outside of the MBNMS) to conduct the research, as it may be difficult to get important information about sampling procedures and data management once the project is suspended. It is also important to ensure that if experimental plots may need to be re-sampled in the future, they are adequately marked and mapped for relocation. Periodic maintenance of experimental plots and markers should also be conducted. All of this will result in a more efficient transition if a new individual resumes the long-term monitoring.

Sampling Modifications

The goal of this particular project was to assess recovery rates and processes in a mid-high intertidal red algal, *Mytilus*, and surfgrass assemblage following the shipwreck of the F/V Trinity (1996) at Pt. Piños in Monterey Bay. If the MBNMS was particularly interested in the recovery of the characteristic organisms with each assemblage, the sampling scheme could be modified to target those species. For example, if the MBNMS was specifically interested in assessing the abundance of surfgrass, mussels, and the dominate red algal species in the high intertidal zone (*Endocladia muricata*, *Mastocarpus papillatus*, and “*Petrocelis*”) that occupy each of the three zones, and not the

successional processes and species that affect the return to these climax species, the sampling protocol could be simplified to exclude all other organisms.

Our results indicate that the surfgrass and *Mytilus* assemblages are still recovering. *Phyllospadix* and tunicates commonly associated with the undisturbed surfgrass assemblage just re-colonized disturbed areas. Continued monitoring of these later successional species would serve as a good proxy for the overall recovery of the surfgrass assemblage. Similarly, *Mytilus* re-colonized the mid intertidal at a slow rate. While other species occupy the zone, if the health or recovery of this assemblage is characterized by the abundance of *Mytilus*, then sampling just for this species seems like an effective manner to assess recovery.

By focusing on the dominant species within each assemblage it would be possible to more easily maintain a long-term monitoring program at this site and in general. This is primarily because the experimental plots would take less time to survey and if only a few characteristic species were targeted, a less skilled person could sample plots. Currently, effective sampling can only be conducted by a person who is familiar with the extremely diverse marine flora of the Monterey Bay. The red algal and surfgrass assemblages are particularly time consuming to sample because the diversity of algae in those assemblages. These suggestions are of course only practical if the project goal is focused on the dominant species that occupy each assemblage, and should not be employed if the processes and intermediate successional phases associated with recovery are of interest.